

The Fossil Pollen Record of the Pandanaceae

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Abstract

The fossil record of pollen comparable to the family Pandanaceae and sometimes directly comparable with the extant genus *Pandanus* extends back to the latest Upper Cretaceous. The family which once had a wide geographic distribution on all continents except Australia, has, since the mid-Tertiary, become restricted to the Old World tropics and subtropics.

Introduction

The monocotyledon genus *Pandanus* Rumph. ex L. comprises about 600 species of trees, shrubs and less frequently subshrubs. Several, such as *P. epiphyticus* Martelli and *P. alticola* Holt. and St. John from Malaya and Borneo are truly epiphytic though facultatively so, also occurring on boulders of limestone or sandstone (Stone, 1978). The tree habit is the most common, and such pandans form a conspicuous part of the vegetation of many tropical shorelines. The pandans (or screw-pines) are distributed throughout the palaeotropics, with species occurring on nearly all tropical and marginally subtropical islands of the Pacific, the northern tropical regions of Australia, tropical Southeast Asia, Indonesia, the Philippines, southern India and islands of the Indian Ocean, the Malagasy Republic and East and West Africa (Stone, 1976). The genus does not occur naturally in the neotropics. Map 1 illustrates the overall distribution of the genus, as well as the known fossil pollen reports of Pandanaceae.

The pandans are dioecious, with the staminate plants, particularly of the forest species, being less frequently collected than the pistillate plants, due to the brief, ephemeral staminate anthesis. The leaves, usually long, linear, spirally arranged and congested along branch tips, the characteristic stout aerial prop roots, and the often (but not always) large pendulous female cephalia (syncarps) allow recognition of the genus even at some distance.

The pulpy fruits (drupes or polydrupes) are often a bright-coloured red, orange or yellow and are dispersed not only by birds and fruitbats, but within several sections of the genus by ocean or freshwater currents (Stone, 1976). The fruits of *Pandanus helicopus* Kurz which occur today in Bangka Island, Malaya, Borneo and Sumatra, are eaten and thus dispersed by fish and turtles (Ridley, 1930; Stone, 1976). Turtles no doubt also perform a dispersal role for *Pandanus aquaticus* F. Muell. in Australia (Stone pers. comm., 1978). The small, and very light fruits of *Pandanus basedowii* C.H. Wright, native in the Northern Territory of Australia may be distributed by wind (Stone, 1974).

Pollen Morphology

The pollen of *Pandanus* (29 species examined) is free, radiosymmetrical, spherical to ovoid (often irregular) monoporate (rarely pseudocolpate). The ornamentation is typically echinate but some species are psilate, finely granulate or finely rugulate (e.g. granulate in *Pandanus dorystigma* Mart.; rugulate in *P. matthewsii* Merr.; psilate in *P. julianettii* Mart. and *P. elöstigma* Mart.). The echinae are conical, blunt tipped or capitate, and range in length from $<1.0\ \mu$ to $4.5\ \mu$. They are more or less evenly distributed over the surface of the grain. The pore (often difficult to observe) is circular and situated at one end of the long axis, with either an entire or diffuse margin, annulate or non-annulate, diameter $2.4\ \mu$ (rarely larger). The exine is two-layered. In some species the sexine is thicker than the nexine, while in other species the opposite is true. Wall thickness ranges from $<1.0\ \mu$ to ca. $1.5\ \mu$. Dimensions for 29 species examined are $16\ (22.2)\ 37\ \mu \times 13\ (17.1)\ 25\ \mu$.

Studies on the pollen morphology of Pandanaceae include: Erdtman (1972), Huang (1970), Huynh (1980), Selling (1947), Sharma (1968), and Sowunmi (1974).

Comparisons with other extant Pollen Forms

Several angiosperm families have genera with certain pollen-morphological similarities to *Pandanus*. Sharma (1968) placed significance on the monocolpate condition of *P. odoratissimus* L.f. as providing evidence of palynological affinity of *Pandanus* with *Hypoxis* (Hypoxidaceae) and *Smilax* (Liliaceae). *Hypoxis* pollen (12 species examined) is monosulcate, often foveolate, has a rather thick exine and the grains measure about $50\ \mu$ in diameter. *Smilax* is non-aperturate, or monosulcate, but never monoporate; the exine is tenuiexinous (nexine thinner than sexine). *Pandanus* pollen may be quite easily differentiated from either of these two genera. *Pandanus* pollen is much smaller than that of *Hypoxis*, and is never foveolate; the presence of a pore (if discernable) will exclude *Smilax*, and in spinate forms of *Pandanus* the nexine is thicker than the sexine.

In the family Araceae, the genus *Remusatia* has pollen which superficially resembles that of *Pandanus*, but upon closer examination can be easily distinguished. Although the sculpturing elements in *Remusatia* are echinate, interestingly the spines are of two distinct sizes and shapes. The larger spines, as wide as they are high are interspersed with much smaller spines somewhat longer than wide. This distinctive feature, not observed in *Pandanus*, as well as the non-aperturate condition of *Remusatia* allows easy recognition of its pollen.

The generally larger diameter and extremely small scrobiculi (very small, more or less circular pits) differentiate *Joinvillea* (Flagellariaceae) pollen from that of *Pandanus*.

Although a number of palm genera (e.g. *Arenga*, *Manicaria*, *Maurita*, *Socratia* et al.) have spherical, echinate pollen, none are monoporate.

As far as is known, only three dicotyledon genera have pollen which might be confused with that of *Pandanus*.

The pollen of *Peumus* (monospecific genus of the Monimiaceae) much resembles that of *Pandanus*, but the grains are inaperturate, and the bases of the spines do not appear sunken below the surface, a feature common to *Pandanus* pollen. The size of *Peumus* pollen ranges 38-41 μ , somewhat larger than that of *Pandanus*.

Hernandia (Hernandiaceae) pollen although echinate can not be confused with that of *Pandanus*, because of its larger size (generally up to 90 μ), the equidimensional spines, and granulate surface between spines.

Stachyanthus (Icacinaceae) has inaperturate, spinose pollen. The characteristic, long (up to 4 μ), recurved spines however allow recognition of this pollen as distinct from *Pandanus*.

The Fossil Occurrences

Forty-five references to fossil pandanaceous pollen are to be found in the published literature (table 1). Thirty-five of these are Tertiary or younger occurrence, eight of which occur within the present distribution of the genus (the paper by Leopold, 1969, contains four localities, thus there are 11 fossil occurrences shown on map 1 within the present range of *Pandanus*). The combined stratigraphic ranges of fossil Pandanaceae pollen from major geographic regions of the world are illustrated in graph 1.

The stratigraphically oldest reports of pollen referable to the family Pandanaceae, are from the Maestrichtian of the western interior of North America. Oltz (1969) reported its occurrence from the Hell Creek and Tullock Formations (Maestrichtian-Palaeocene) of central Montana; Norton and Hall (1969) described *Spinamonoporites typicus* Norton from the Maestrichtian and Palaeocene of the type Hell Creek Formation, Montana, which they compared with question to *Pandanus*, and Leffingwell (1971) recovered *Pandaniidites radicus* Leffingwell from the Lance and Fort Union Formations (Maestrichtian-Palaeocene) of Wyoming.

Within the Canadian western interior, pollen referable to the family Pandanaceae occurs in the Palaeocene of Alberta (Snead, 1969) and in the Maestrichtian of the Morgan Creek badlands of southern Saskatchewan (Jarzen, 1978). This latter occurrence is accepted as the oldest record of *Pandanus* pollen (Muller, 1981).

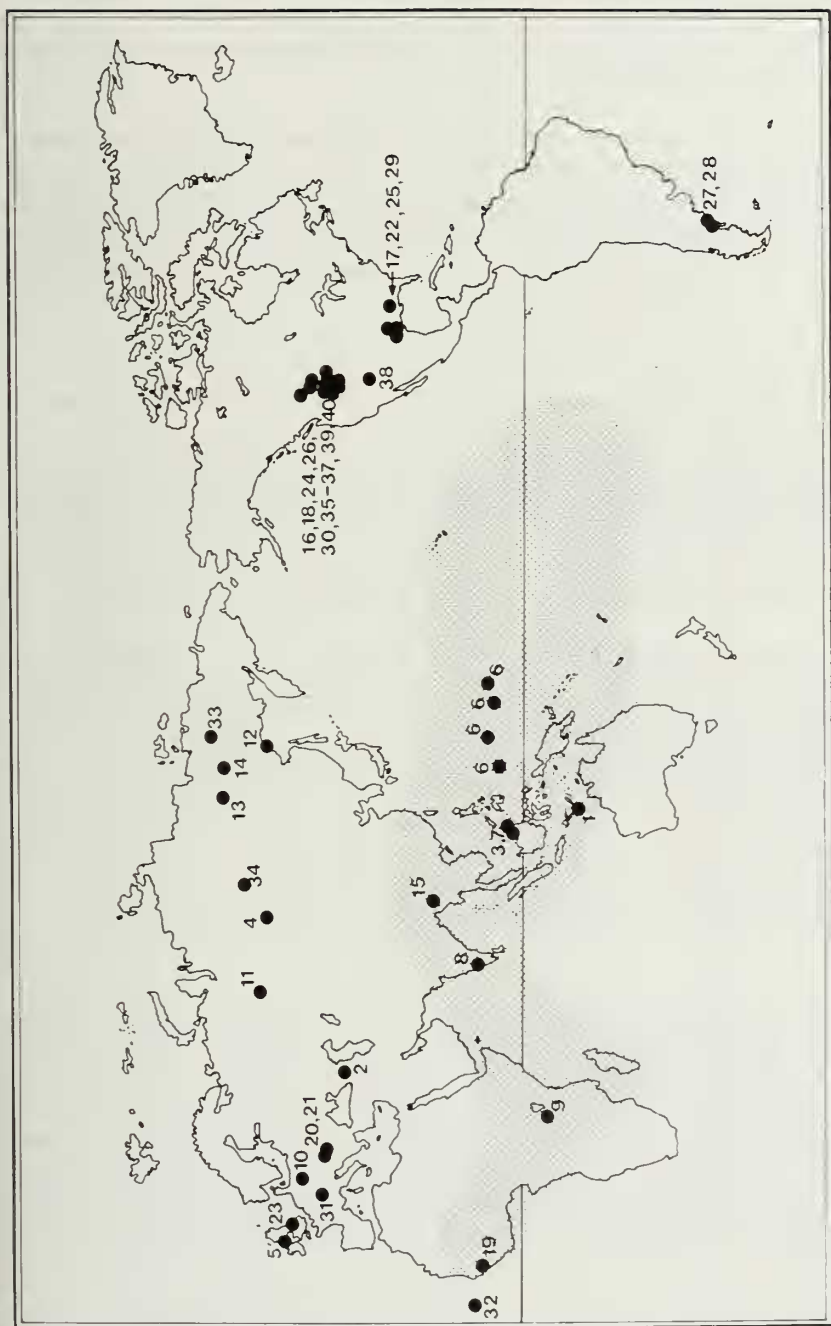
Archangelsky (1973; 1976) described but did not name a species of *Pandaniidites* from the Salamanca Formation (Palaeocene) in the Chubut Province of Argentina, which he compared directly to the genus *Pandanus*. The reports of Archangelsky are the only known occurrences of fossil *Pandanus* pollen from South America. Reports of pollen referable to *Pandanus* from European sediments are those of Raukopf (1959), Kedves (1963), Kedves and Endredi (1963; 1965), Martin (1976), Zaklinskaya (1967) and Simpson (1961) who described ?*Pandanus shiabensis* from the inter-basaltic lignites of Shiaba, Island of Mull, Scotland. Simpson had earlier (Simpson, 1936) assigned this pollen form to the extant genus *Smilax* but after a re-examination, felt it more closely resembled *Pandanus*.

Table 1. Published reports of fossil pollen referable/comparable with the family Pandanaceae. (numbers in parenthesis refer to numbers on map 1).

AUTHOR(S)	LOCALITY	AGE
Zaklinskaya, 1978a (1)	S262 DSPP, Timor	Pliocene-Pleistocene
Shatilova, 1964, 1967 (2)	Georgian, USSR	Pliocene-Pleistocene
Anderson and Muller, 1975 (3)	Northwest, Borneo	Holocene and Miocene
Mchedlishvili 1963 (4)	USSR	Upper-lower Pliocene
Simpson, 1961 (5)	Shiba, Mull Scotland	Miocene or lower Pliocene
Leopold, 1969 (6)	Eniwetok & Bikini Atolls, Guam & Palau Islands	Miocene
Muller, 1964 (7)	Northwest Borneo	Upper Miocene
Rao & Ramanujam, 1975, 1976 (8)	Kerala, India	Lower to Middle Miocene
Sah, 1967 (9)	Burundi	Upper Neogene
Raukopf, 1959 (10)	Eastern Germany	Oligocene-Miocene
Li, <i>et al.</i> , 1967 (11)	Trans-Urals, USSR	Oligocene, Miocene
Sedova, 1956 (12)	Primorsk Kray, USSR	Oligocene
Tarakanova, 1965 (13)	Siberia, USSR	Eocene-Oligocene
Aristova, 1973 (14)	Siberia, USSR	Eocene-Oligocene
Potonič, 1960 (15)	Kalewa, Burma	Eocene
Fisk, 1976 (16)	Wyoming, USA	Eocene
Tschudy, 1973a (17)	Mississippi embayment, USA	Eocene
Love, <i>et al.</i> , 1978 (18)	Wyoming, USA	Middle Eocene
Zaklinskaya & Prokof'yev, 1971 (19)	Guinea	Lower to Middle Eocene
Kedves, 1963 (20)	Hungary	Lower Eocene
Kedves and Endredi, 1963, 1965 (21)	Hungary	Lower Eocene
Elsik, 1967 (22)	Texas, USA	Lower Eocene
Martin, 1976 (23)	England	Palaeocene-Eocene
Bebout & Traverse, 1978 (24)	North Dakota, USA	Palaeocene-Eocene
Fairchild & Elsik, 1969 (25)	Gulf Coast, USA	Palaeocene-Eocene
Jarzen, 1982 (26)	Saskatchewan, Canada	Palaeocene
Archangelsky, 1973, 1976 (27)	Chubut, Argentina	Palaeocene
Petriella & Archangelsky, 1975 (28)	Chubut, Argentina	Palaeocene
Elsik, 1968 (29)	Texas, USA	Palaeocene
Snead, 1969 (30)	Alberta, Canada	Palaeocene
Zaklinskaya, 1967 (31)	Europe	Palaeocene
Zaklinskaya, 1978b (32)	Cape Verde Rise	Cretaceous-Palaeogene
Sedova, 1960 (33)	Far East, USSR	Upper Cretaceous-Danian
Khlonova, 1971 (34)	USSR	Maestrichtian-Danian
Oltz, 1969, 1971 (35)	Montana, USA	Maestrichtian-Palaeocene
Norton & Hall, 1969 (36)	Montana, USA	Maestrichtian-Palaeocene
Leffingwell, 1971 (37)	Wyoming, USA	Maestrichtian-Palaeocene
Tschudy, 1973b (38)	New Mexico, USA	Maestrichtian-Palaeocene
Leffingwell, <i>et al.</i> , 1970 (39)	Wyoming, USA	Maestrichtian
Jarzen, 1978 (40)	Saskatchewan, Canada	Maestrichtian

The first report of fossil pollen comparable to *Pandanus* (or inferred to be *Pandanus* by reference to the family Pandanaceae since the other members of the family, *Freycinetia* and *Sararanga*, are not usually echinate except two *Freycinetia* species which have echinate pollen) is that of Sedova (1956) who designated *Pandanus* sp. from the Oligocene of Primorsk Kray, U.S.S.R.

The geologically most recent occurrences of fossil Pandanaceae pollen are of Pliocene-Pleistocene age deposits of the U.S.S.R. (Shatilova, 1964; 1967) and from



Map 1. Present-day geographic distribution of the Pandanaceae (stippled). Known published reports of fossil pollen referable to the family Pandanaceae (black dots). Numbers refer to numbers in Table 1.

core material of Site 262 drilled by the *Glomar Challenger* in the Timor Trough near the Island of Timor (Zaklinskaya, 1978a). Zaklinskaya refers only to the family Pandanaceae, and does not illustrate the pollen thus assigned. It is probable that the pollen recovered by Zaklinskaya represents *Pandanus* inasmuch as the other two genera within the family usually have psilate exines and would be rather difficult to assign to the family Pandanaceae.

Of the numerous reports of pandanaceous megafossils, nearly all have subsequently been determined to be *Nypa* (Tralau, 1964), and in fact Stone (1976) considers the report of *Pandaniites rhenanus* Krausel and Weyland (1950) from the Oligocene of Germany as a true pandan. The megafossil record of Pandanaceae is thus meager and provides little information on the geologic history of the family.

Discussion

The fossil pollen grains illustrated in plate 1, figures 1–5, were recovered from the uppermost Cretaceous (Maestrichtian) Frenchman Formation of southwestern Saskatchewan, Canada (Jarzen, 1978). These grains were selected to illustrate several features which are diagnostic of extant Pandanaceae pollen. Figure 1 illustrates the general shape (ovoid), circular pore with entire margin and the conical isometric echinae (spines) typical of many species of *Pandanus*. These features are comparable with those of *P. longicaudatus* Holtt. and St. John as illustrated in figure 11.

The fossil grain in figure 2 was photographed in optical section to illustrate the nature of the spine bases which are depressed into the interior of the pollen wall (see also Erdtman, 1972, p. 308, fig. 179A). This feature of “sunken bases” is clearly seen in the phase contrast photomicrograph (fig. 7) of *Pandanus tectorius* Sol. and as faint protuberances in the electron micrograph (fig. 13) of *P. vandra* St. John.* Figure 3 also illustrates the “sunken bases” of the spines but additionally shows the less frequent annulate pore condition of some of the fossil grains. *P. odoratissimus* L.f. (fig. 8-9) also displays an annulate pore. *Pandaniidites radicus* Leffingwell (1971), recovered from the Maestrichtian of Wyoming, and *P. texus* Elsik (1968) are clearly annulate.

The fossil grain type illustrated in figure 4 is rarely encountered in Saskatchewan sediments. The unique elongated, clavate spines were initially considered unlike the usual conical spines of *Pandanus*. However, as illustrated in figure 12 the pollen of *P. mozambicus* St. John bears identical spines. Figure 5 and figure 10 illustrate the rather rare monocolpate condition in the fossil specimens (fig. 5) and extant *Pandanus tectorius* Sol. (fig. 10). Figure 14 illustrates spine shape in modern *Pandanus*, with a bulbous enlarged base. This feature may or may not occur at random on certain fossil specimens. Some of the spines on the fossil grain in figure 2 approach this condition.

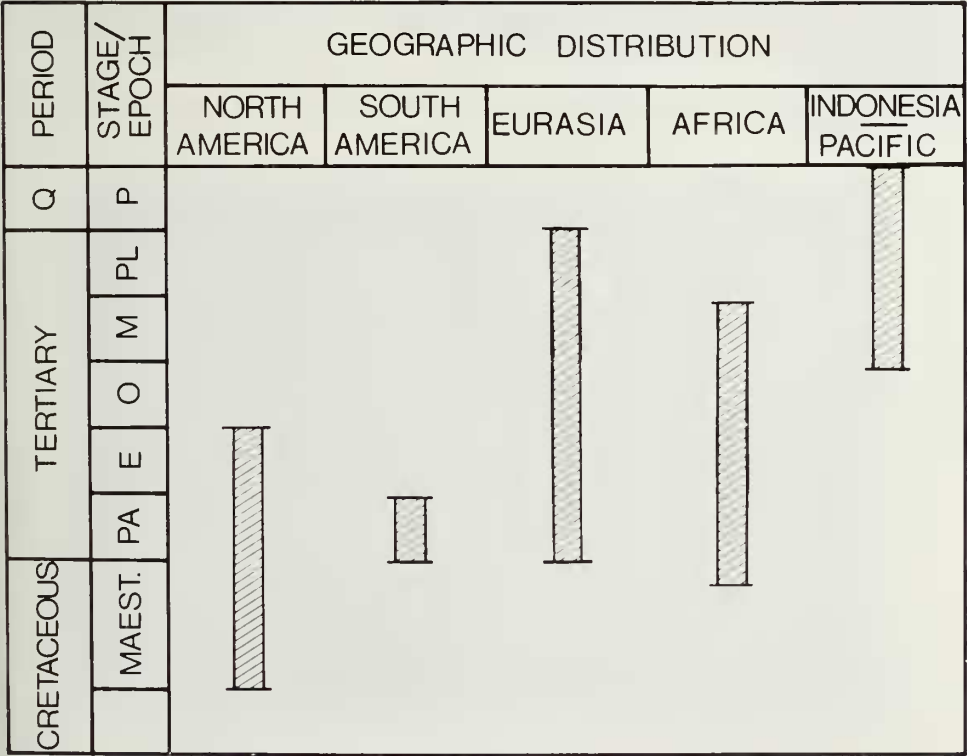
There is little doubt as to the validity of reports of fossil pollen referable to the family Pandanaceae from the Tertiary period (see map 1) and especially so for

* *P. vandra* St. John is regarded by Stone (pers. comm., 1983) as an undoubted synonym of *P. tectorius* Sol.

those occurrences within the present range of *Pandanus*. Less confidence is held for the uppermost Cr taceous occurrences, since all of these reports occur outside the present geographical range of the family.

Stone (1976) and Muller (1981), accept palynological reports of Maestrichtian Pandanaceae pollen. From the descriptions and illustrations of the six published reports of "pandanaceous" pollen from the Maestrichtian/Palaeocene interval of the western interior of North America it appears that at least two species of the family Pandanaceae once occurred in North America 65-63 million years ago. Since the Cretaceous, continental movements, withdrawal of the eperic seaways, mountain building, and changes in climate have dramatically reduced suitable conditions for the survival of the Pandanaceae in North America. Today no wild plants of the family occur in North or South America, Europe, or temperate Asia where mega- and micro- fossils have been recovered (Stone, 1976). Speculation as to the origin of the family Pandanaceae should accept as baseline data the reports of fossil Pandanaceae from North and South America, which must be considered valid.

Jarzen (1978) has suggested a modern analogous environment for the fossil flora recovered from the Maestrichtian of the Morgan Creek badlands of Saskatchewan as being in the Southeast Asia-Indomalaysian area based on the occurrence of several



Graph 1. Generalized stratigraphic and geographic distribution of reports of fossil Pandanaceae pollen.

diagnostic pollen taxa, including that of Pandanaceae. Other angiosperm pollen recovered from the Morgan Creek sediments could be compared with extant families including the Juglandaceae, Myrtaceae, Buxaceae, Cercidiphyllaceae, Gunneraceae, and all found together today only in Southeast Asia-Indomalaysia.

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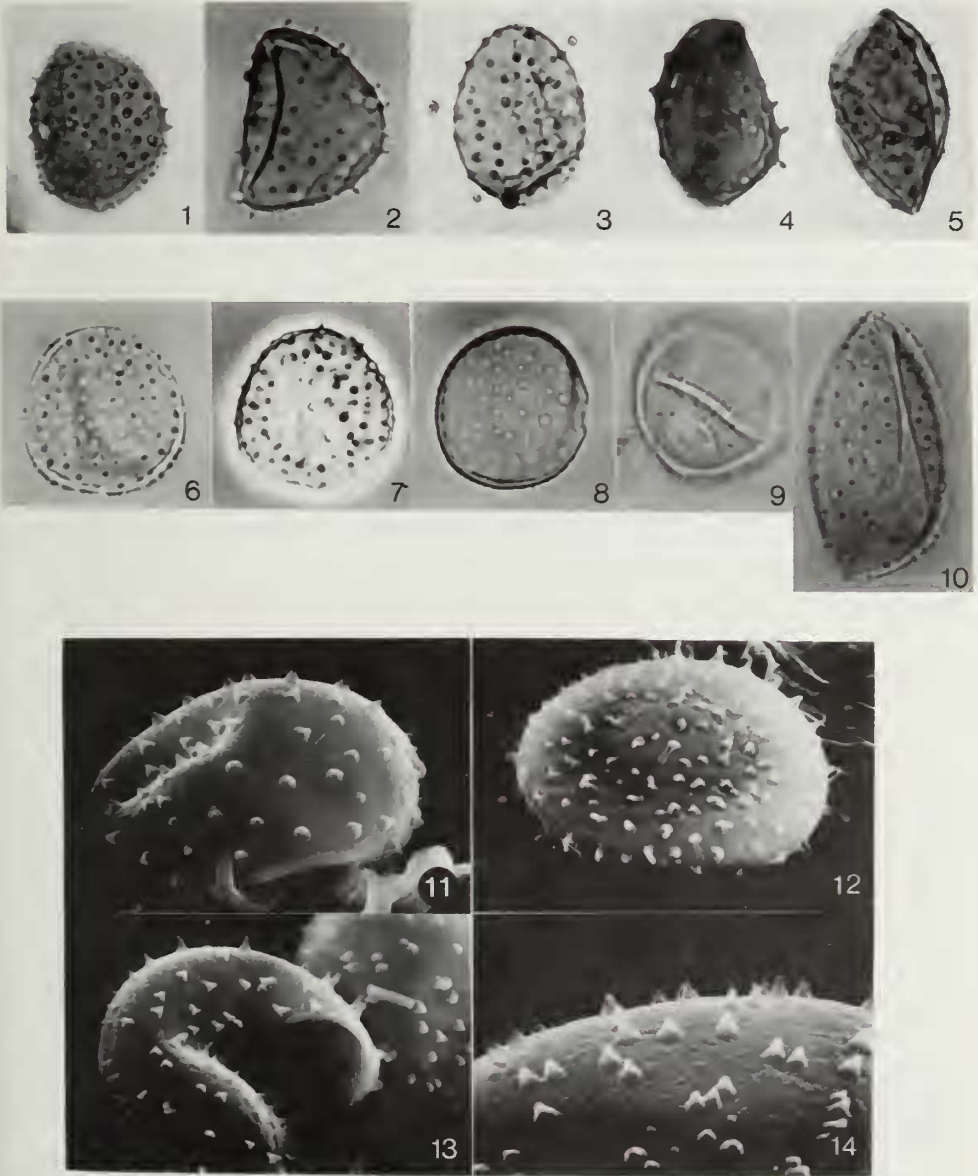
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Plate 1. Morphological variation in extant and fossil Pandanaceae pollen. Fig. 1. Fossil grain illustrating the "normal" conical shaped spines (11/03 - 86.3 × 36.9). Fig. 2. Fossil grain showing, in optical section, the bases of spines sunken into the interior of the grain (11/07 - 81.3 × 37.3). Fig. 3. Fossil grain with annulate pore (07/04 - 95.4 × 36.8). Fig. 4. Fossil grain with club-like ornamentation (11/04 - 89.0 × 35.6). Fig. 5. Fossil grain in colpate condition (11/03 - 82.9 × 35.5). Fig. 6. *Pandanus tectorius* Sol., bearing the "normal" conical spines (10513 - 88.2 × 41.6). Fig. 7. *P. tectorius* Sol., photographed in phase contrast to illustrate sunken bases of spines into interior of grain (10513 - 88.2 × 41.6). Fig. 8. *P. odoratissimus* L.f., with annulate pore as observed in optical section (228 - 93.1 × 40.6). Fig. 9. *P. odoratissimus* L.f. annulate pore observed in surface view (228 - 93.2 × 39.9). Fig. 10. *P. tectorius* Sol., in colpate condition (227 - 95.3 × 31.5). Fig. 11. *P. longicaudatus* Holtt. & St. John, illustrating the conical shaped spines (7371-SEM 012/7). Fig. 12. *P. mozambicus* St. John, with club-like ornamentation similar to fossil grain in Fig. 4. (870-SEM 003/10). Fig. 13. *P. vandra* St John, split open to show sunken bases of spines into interior of grain (872-SEM 001/1). Fig. 14. *P. furcatus* Roxb. detail of surface showing spines with enlarged bases (7369-SEM 011/7). Figs. 1-10: X 1,000; Figs. 11, 12: X 2,500; Fig. 13: X 2,200; Fig. 14: X 3,400.

Plate 1

Morphological Variation in Extant and Fossil Pandanaceae Pollen



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